Salmonberry Clonal and Population Structure: The Basis for a Persistent Cover

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SALMONBERRY CLONAL AND POPULATION STRUCTURE: THE BASIS FOR A PERSISTENT COVER[1]

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Abstract. To understand how populations of salmonberry (*Rubus spectabilis*) persist in common forest stand types, we studied the above- and belowground structure of salmonberry clones and populations in upland alder and conifer stands, in riparian stands, and in 2-yr-old and 13- to 18-yr-old clearcuts in the central Oregon Coast Range. On undisturbed sites individual clones and populations replace aerial stems by rhizome extension, by production of new genets, and by sprouts from buds on old aerial stems. It appears that frequent initiation of aerial stems from these three sources enables salmonberry populations to persist and maintain a dense cover. The size distribution of aerial stems on these sites resembled that of an uneven-aged stand of trees, with stem numbers decreasing from small to large size classes. Within the first two growing seasons after disturbance to overstory trees and the understory, salmonberry populations maintained themselves by a rapid initiation of new rhizomes (1.0–2.5 m/m^2 annually) and aerial stems (25–50 stems/m^2). These populations apparently continue to grow well, since the greatest rhizome and aerial stem biomass occurred in 13- to 18-yr-old clearcuts with no overstory trees.

Rhizome density of salmonberry populations, as well as rhizome and aerial stem biomass, was significantly and negatively related ($r^2 = 0.71$–0.83) to the basal area of overstory trees. It appears that population structure, rhizome length and aerial stem, rhizome, and total biomass, can be predicted from measures of preharvest overstory trees, and also from salmonberry stem number and basal area.

Clonal architecture varied with stand type. Salmonberry clones in alder stands were larger (18 m total rhizome) than those in conifer stands and on riparian sites (5–6 m rhizome). Clones in alder stands also produced more ramets and more aerial stems than those in conifer and riparian stands.

Key words: clonal architecture; clonal populations; clones; Douglas-fir forests; forest disturbance; forest regeneration; forest succession; persistent cover; red alder stands; rhizomes; Rubus spectabilis; understory.

INTRODUCTION

Salmonberry (*Rubus spectabilis* Pursh) is a common clonal shrub occurring in a range of stand types within the forests of the Pacific Northwest. It is particularly abundant in red alder (*Alnus rubra* Borg), where it forms dense, continuous understories (Carlton 1988). It occurs in patches beneath canopy openings in Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) (Franklin and Dyrness 1973), and is very common on periodically flooded riparian sites with mixed red alder/conifer overstories (Henderson 1970).

Salmonberry persists for many years in these stand types (Newton et al. 1967, Carlton 1988). It also sprouts vigorously from buds on rhizomes and at the base of its aerial stems, and within 2–3 yr after severe distur-

bance to the overstory, it produces pure, dense stands (30 000+ stems/ha, 2+ m tall) (Allen 1969). Once it forms a cover in the open or in the understory, it has a profound effect on forest succession; even shade-tolerant trees such as western hemlock have difficulty becoming established, as do tall shrubs such as vine maple (*Acer circinatum* Pursh.) and elderberry (*Sambucus racemosa* L.) that might otherwise replace the salmonberry (Franklin and Pechanec 1967, Newton 1978).

A major purpose of this study was to determine how salmonberry is able to persist for many years. For it to persist it must not only rapidly reoccupy a site after disturbance, but it must maintain a canopy dense enough to preclude the establishment of species capable of overtopping it. For a rhizomatous species such as salmonberry, this means continually producing new aerial stems and ramets to refill canopy openings caused by dead and broken aerial stems. Cook's (1985) review

TABLE 1. Description of salmonberry study sites under hardwood and conifer stands and on clearcuts in western Oregon forests.

Stand type*				Salmonberry populations			
	Species	Age (yr)	Basal area (m²/ha)	Aerial stem (no./m²)	Basal area (cm²/m²)	Total biomass (kg/m²)	Canopy height (cm)
A	Alder	45	26	8.4	9.0	1.60	250
A	Alder	50	21	10.3	9.2	1.86	240
A	Alder	55	30	6.4	7.5	1.40	300
A	Alder	53	30	3.9	6.1	1.62	340
C	Douglas-fir, hemlock	130+	51	2.5	2.7	0.39	201
C	Douglas-fir	140	38	3.5	4.2	0.84	230
C	Hemlock, Douglas-fir	150	54	4.0	8.7	0.55	320
C	Douglas-fir	180	34	3.3	9.6	1.05	260
R	Alder, Douglas-fir	50	18	10.0	6.3	1.01	210
R	Alder, Douglas-fir	60	35	7.0	3.5	0.64	200
R	Alder, hemlock	60	16	4.0	6.2	1.66	320
R	Hemlock, spruce	120	65	2.3	2.8	0.38	280
Y	Young clearcut	2	0	26.6	19.0	2.04	160
Y	Young clearcut	2	0	37.0	15.7	2.31	150
Y	Young clearcut	2	0	52.0	16.7	1.06	140
Y	Young clearcut	2	0	37.8	13.5	0.87	80
O	Older clearcut	15	0	8.5	22.1	4.62	380
O	Older clearcut	18	0	5.8	23.7	6.13	330
O	Older clearcut	13	0	13.1	27.3	5.00	300
O	Older clearcut	13	0	19.8	22.8	3.41	340

The top of the table has a spanning header "Overstory" over the Species, Age, and Basal area columns, and "Salmonberry populations" over the remaining four columns.

* Stand type R is riparian; others are on upland sites.

of clonal growth and development suggests that ramet initiation and death rates are relatively constant through time in stable communities. If dead or damaged aerial stems are replaced at a rate that inhibits taller or more competitive species, salmonberry communities may be stable over long periods. Kurmis and Sucoff (1989) have shown that populations of a rhizomatous forest shrub are able to maintain a dense canopy for many years by a continual input of new aerial stems. In addition, Balogh and Grigal (1987) found that age distributions of aerial stems in communities of rhizomatous shrubs were best described by a negative exponential model, and they hypothesized that the slope of the model represents mortality rates, while the intercept represents input of aerial stems. Although a large bank of salmonberry seeds is present on some sites (Ruth 1970), seedling occurrence is rare in established salmonberry communities. Thus, persistence of salmonberry cover appears to be related primarily to stem longevity and vegetative propagation of new stems.

Other objectives of this study were to determine whether salmonberry clonal architecture and population structure were affected by environment and whether rhizome density and biomass could be predicted from the density of overstory trees and salmonberry aerial stems (Maxwell 1990). Bell and Tomlinson (1980) reviewed the literature on the architecture of rhizomatous plants and concluded that the rate of clonal development varies among environments, but that the architecture is relatively similar. We measured some aspects of clonal architecture and population structure

in five types of stands to understand how salmonberry maintains a persistent cover and to test Bell and Tomlinson's hypothesis. We also used these data to see whether salmonberry population development could be predicted for a range of environments (Maxwell 1990).

METHODS

Site selection

We selected 20 study sites on slopes <20% on the west side of the central Oregon Coast Range, four in each of five different stand types. All stand types except Type R were upland: Stand Type A—alder; Type C—conifer; Type R—riparian; Type Y—young clearcuts (2 yr old); Type O—older clearcuts (13-18 yr old) that had not been stocked with conifers. Each salmonberry community had an 80-100% crown closure and extended over at least 0.5 ha. On the clearcut sites, the overstory had been removed by cable logging, and there was no disturbance to the forest floor or to salmonberry rhizomes, and no evidence of disturbance since clearcutting. Overstory conifers and hardwoods on the forested sites were at least 45 yr old, and there had been no apparent windthrow, fire, logging, or other disturbance to the overstory trees or the salmonberry. Vegetation was representative of the western hemlock/salmonberry association of the central Oregon Coast Range (Franklin and Dyrness 1973, Hemstrom and Logan 1984). Density of overstory trees was typical for these species and locations (Table 1).
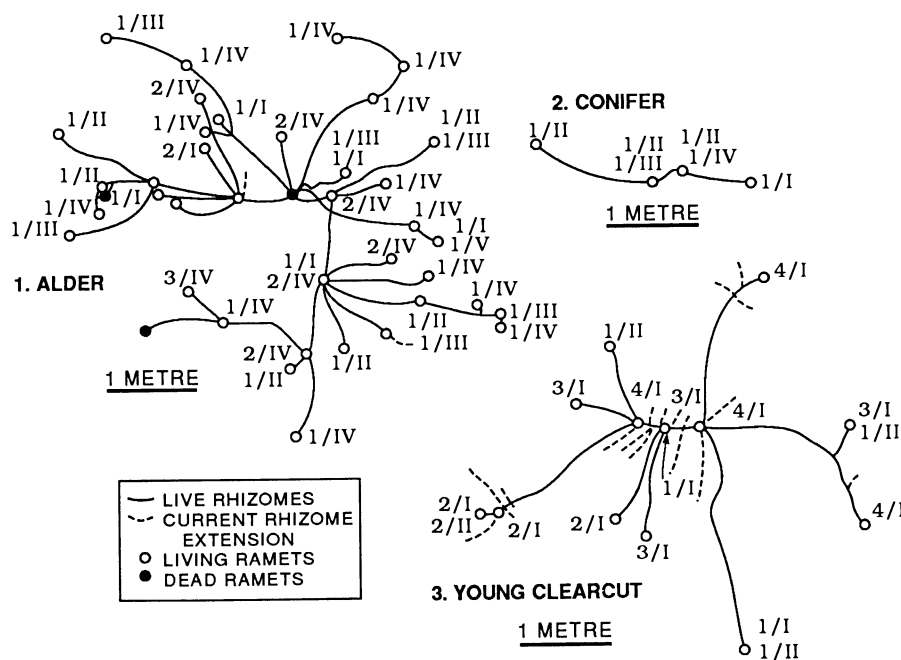
FIG. 1.   Typical examples of salmonberry clones from alder, conifer, and young clearcut stands. Numbers indicate number of live aerial stems, by condition class (Classes I–IV, where I is the youngest). See *Methods: Salmonberry clones* for description of condition classes.

Salmonberry clones

We excavated 3–7 salmonberry clones from each site in the first four stand types, a total of 70 clones. We did not attempt to examine clones in the older clearcuts since the dense mass of rhizomes made tracing individual clones difficult. For each clone (ramets that are attached to the same rhizome system) we randomly chose a ramet and removed the soil around it; we then traced the rhizomes of the entire clone (Fig. 1). Rhizomes and ramets were mapped on a grid. We counted aerial stems and measured their length. We measured the rhizome lengths between ramets and summed them to determine total rhizome length per clone. We quantified rhizome density and branching pattern by placing a circular grid divided into four quadrants over each mapped ramet and counting the number of rhizomes initiated in each quadrant. We estimated annual rhizome extension and production by measuring the length of the white unsuberized rhizomes on which buds and leaf scales were still visible and counting the number of actively growing apices. We could not age the pithy aerial stems (Barber 1976) by counting xylem rings or bud scars, so we tallied them by condition class: Class I—current to 1 or 2 yr old, bright green, spines rigid and firmly attached; Class II—brown or tan stems, spines brittle and sloughing off; Class III—smooth bark, no spines; Class IV—rough bark, covered with moss. These classes represent a relative age sequence, since we were not able to assign exact ages. Class IV stems are probably older than 10 yr, however.

Salmonberry populations

At each of our 20 sites, we described salmonberry populations on three 2 × 2 m plots adjoining the area where clones were excavated. On each plot, we measured salmonberry canopy height and recorded numbers of stems by 0.5 cm diameter classes. We then attempted to excavate all rhizomes and determined the number of clones within the plot. Rhizomes were traced 2 to 3+ m beyond the plot to identify individual clones, but clones were not entirely excavated. Rhizomes were washed to remove soil. In the laboratory, we measured total rhizome length, annual rhizome extension, number of ramets, and biomass after oven drying (80°C for 48 h). Aboveground biomass was estimated from the following equation relating total stem dry mass y (in grams) to stem diameter d (in centimetres), which was developed from a sample of 2–3 aerial stems from each site:

$$\log y = 4.078 + 3.383 \log d;\; r^2 = 0.91.$$

Basal area of the overstory trees was measured on a 20 × 20 m plot surrounding each 2 × 2 m plot.

Data analysis

We used analysis of variance and Tukey's LSD ($P \leq .05$) to compare mean clonal characteristics of the five types of stands. We calculated rhizome relative growth rate (annual growth percent) for each clone and plot by dividing the total length of the new rhizomes by the length of the older ones. Data from the three
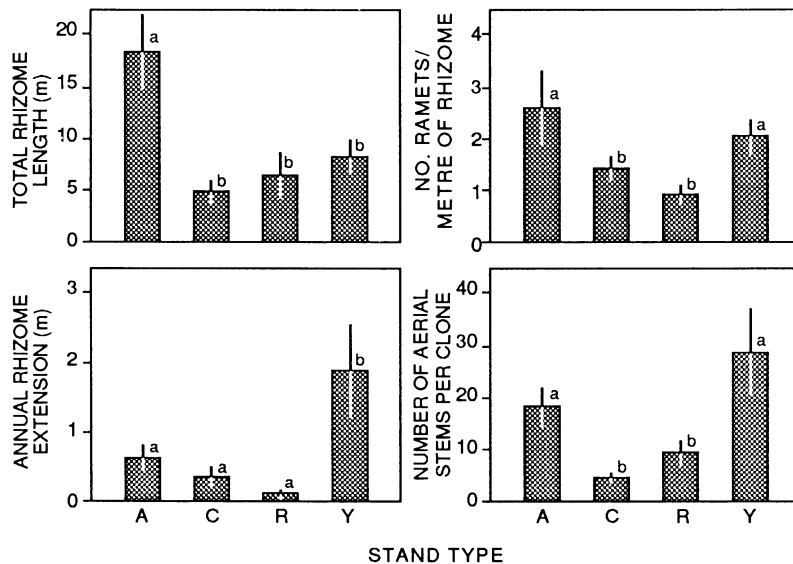
FIG. 2.   Salmonberry clone characteristics by stand type: A = alder, C = conifer, R = riparian, Y = young clearcuts. Data are means ± SE. Means sharing the same letter are not significantly different ($P \leq .05$, ANOVA followed by Tukey's LSD).

plots in each stand were analyzed in a nested design with stands nested in types to compare total, rhizome, and aerial stem biomass; rhizome length; annual rhizome extension; ramet density; stem number; and stem frequency per diameter class for the five stand types (Snedecor and Cochran 1967). Stem frequency data were transformed (arcsine) to ensure a normal distribution. The other data were analyzed after log transformation to homogenize the variation and to improve the distribution of the variables. To see whether population structure could be modeled, we averaged data from the three plots in each stand and used regression analysis to relate dependent variables (rhizome length and biomass and total salmonberry biomass) to readily measured independent variables (number of salmonberry stems per square metre, and basal area of salmonberry in square centimetres per square metre and overstory trees in square metres per hectare) for each site ($n = 20$). We also analyzed these data on a plot basis ($n = 60$).

RESULTS

Clonal structure

Salmonberry clones are made up of a network of rhizomes connecting ramets that consist of a tap root and 1–5 aerial stems up to 4 m tall. For example, a clone in an alder stand had 36.5 m of rhizome connecting 39 ramets with 75 aerial stems, 80% of them in condition Classes III and IV (Fig. 1). Rhizomes occurred from 2 to 20 cm below the soil surface and supported many fine roots. Although the depth of a particular rhizome was generally consistent over its entire length, some varied in depth by as much as 20

cm. On steep slopes (>50%) adjoining the study sites, we found rhizomes at depths at 1–2 m. Of the 70 clones excavated, 59 appeared to be entire, and all rhizomes were healthy. There was no evidence of rhizome decay or injury indicating that part of the clone had died or become separated. Rhizomes 5–8 cm in diameter were common, suggesting that rhizomes are long lived. Parts of the smaller (0.5–0.7 cm) rhizomes on 11 clones had decomposed, so that we could not identify the entire clones.

Several characteristics of salmonberry clones were related to salmonberry's ability to persist. Clones in all three undisturbed stand types produced 1–2 new rhizomes per year, with an annual extension ranging from 0.1 m in riparian stands to 0.7 m in alder stands (Fig. 2). In these same stand types, clones typically had aerial stems in all four condition classes; however, from 13 to 33% of the aerial stems were in the younger classes (I and II), and were initiated from buds at the base of older aerial stems or from the new ramets produced from rhizomes. Clones in recent clearcuts responded to disturbance by producing an average of seven new rhizomes per clone, and annual rhizome extension was 1.9 m, significantly ($P < .01$) higher than in other stand types. The rhizome growth percent of these clones was 27%, much higher than growth for clones in undisturbed stands (2–6%). Clones in recent clearcuts also had the greatest number of aerial stems (all in Classes I and II); numbers were significantly ($P \leq .05$) more than those in conifer and riparian stand types, but not significantly more than in alder (Fig. 2).

Clonal architecture varied considerably with stand type. Total rhizome length per clone in alder stands averaged 18.3 m, significantly greater than in other

stands (<1.7–8.1 m) (Fig. 2). We observed no "standard pattern" of rhizome production, and between ramets rhizomes tended to be unidirectional. Distance between ramets ranged from 0.2 to 4.45 m, and averaged from 0.72 m in the conifer, riparian, and young clearcuts to 1.02 m in alder stands, but it was not significantly different among types. In undisturbed stand types, rhizomes were initiated only at the base of ramets, while in clearcuts new rhizomes were often initiated at several points along old rhizomes, as well as at the base of ramets (Fig. 1).

Ramet density (ramets per metre of rhizome) was greatest on clones in alder stands and recent clearcuts (Fig. 2), where rhizomes also formed a denser network, as measured by the average number of quadrants in which rhizomes occurred (Table 2). In alder stands and recent clearcuts, an average of 3.7 and 2.7 quadrants around each ramet, respectively, contained rhizomes, significantly ($P \leq .05$) more than on clones in conifer (1.5) and riparian (1.6) stands. Rhizome number per quadrant was also greater in alder, yielding a dense, branched network of rhizomes. Clones in the conifer stands tended to be somewhat linear (Fig. 2), while three clones extracted from a rocky riparian site had produced no rhizomes.

Population structure

Characteristics of salmonberry populations (Fig. 3) were strongly related to stand type. Although there were significant differences among stands within types, 65% or more of the variation in these characteristics was associated with stand type, with the remaining variability accounted for by within-stand differences. Initiation of new rhizomes, ramets, and aerial stems indicated that salmonberry populations could maintain a dense cover.

Salmonberry populations were composed of a coalescence of clones with intermixing of rhizomes below ground and aerial stems above. We found from two to six clones in each of the 60 4-m² plots. Annual rhizome extension was particularly striking in young clearcuts (2.1 m/m²), and it ranged from 0.1 to 0.8 m in the other types (Fig. 3). Expressed as annual growth percent, rhizome extension was significantly greater in young clearcuts (14.3%) than in alder (5%), conifer (3.7%), and riparian (3.5%) stand types. It was least in the old clearcuts (2.3%), where rhizome density was already greatest.

The frequency distribution of salmonberry stems by diameter class was remarkably similar in alder, conifer, riparian, and older clearcut stand types (Fig. 4); this distribution suggests a continual recruitment of new stems. About 10–20% of the stems were 0.0–0.5 cm in diameter, 50–60% were 0.6–1.5 cm, and the remainder (generally in the older Classes III or IV) were 1.6–3.1+ cm.

In recent clearcuts, there were significantly more aerial stems (Fig. 3); 90% of them were <1.0 cm (Fig.

TABLE 2. Description of branching pattern of salmonberry. Number of rhizomes around each ramet (mean and SE; N = 16 clones per stand type).

Stand type	Number of quadrants with rhizomes		Number of rhizomes/ quadrant	
	$\bar{X}$	SE	$\bar{X}$	SE
Alder	3.7	0.13	2.4	0.11
Conifer	1.5	0.13	1.4	0.14
Riparian	1.6	0.07	1.4	0.10
Young clearcuts	2.7	0.30	1.9	0.17
LSD*	0.76		0.56	

* Tukey's least significant difference between means ($P \leq .05$).

4), and all were in Classes I or II. The fewest aerial stems occurred in the conifer stands.

Salmonberry population structure varied among stand types. Significantly greater average rhizome length (15.5 m/m²) was found in the old clearcuts, while the least was found in the conifer stands (Fig. 3). Rhizome length in the young clearcuts (10.5 m/m²) was 2–3 times the length in alder, conifer, and riparian stands. Ramet density was significantly greater in the young (11.0 ramets/m²) and older clearcuts (7.0 ramets/m²) than in the understory of alder (3.9 ramets/m²), conifer (2.0 ramets/m²), and riparian (2.3 ramets/m²) stands.

Biomass (aboveground, rhizome, and total) was significantly greater in the older clearcuts than in the other four stand types (Fig. 3). For example, total biomass averaged 4.25 kg/m² in the older clearcuts, more than 2.5 times as great as in the understory of alder stands (1.62 kg/m²); biomass under alder was significantly greater than in conifer and riparian stands. Below alder, salmonberry apparently allocated more resources to aboveground growth. The ratio of aboveground biomass to rhizome biomass in alder was 4.0, which was greater than in the conifer (2.6), riparian (2.5), and old clearcuts (2.0). This ratio was lowest in young clearcuts (1.2), with their small new aerial stems.

In riparian zones, populations of salmonberry were quite similar to those in alder and conifer stands. Even in stands where hydric plants such as yellow skunk cabbage (Lysichitum americanum Hulten & St. John) were present, there was no evidence that flooding or subsurface water affected salmonberry population development. For example, the relationships of rhizome biomass and length to salmonberry aerial stem number and basal area were similar in riparian, alder, and conifer stands (Figs. 3 and 4).

Although population structure varied among stand types, it appeared to be predictable. Average rhizome length and biomass per square metre in the 20 stands (Fig. 5) and total salmonberry biomass per square metre (Table 3) were strongly related to overstory tree density and salmonberry stem number and density, all easily measured variables. Log rhizome length was negatively and significantly related ($r^2 = 0.81$) to overstory
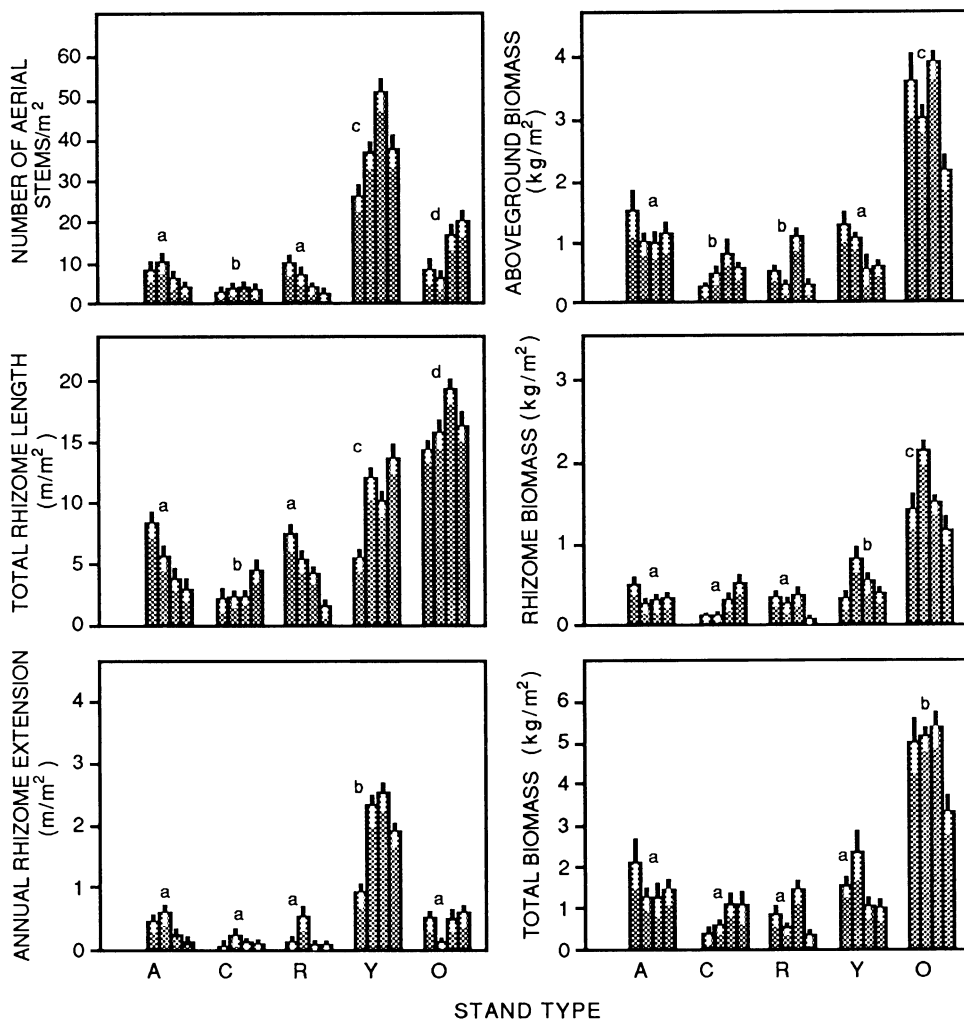
FIG. 3. Salmonberry population characteristics for the sites within each of the five stand types: A = alder, C = conifer, R = riparian, Y = young clearcuts, O = old clearcuts. Data are means ± SE. The same letter indicates that the means for the stand types (not shown) are not significantly different ($P \leq .05$, ANOVA followed by Tukey's LSD).

basal area in all stands combined (Table 3, Fig. 5), and it was also signficantly related to the log of salmonberry stem number and basal area (Table 3). Rhizome biomass per square metre can be best predicted from salmonberry stem basal area ($r^2 = 0.83$). Total biomass (above and below ground) per square metre can be reliably estimated ($r^2 = 0.78$) from salmonberry stem basal area and overstory basal area (Table 3). These relationships were all significant ($P \leq .02$) when calculated for individual plots ($n = 60$). However, the variability ($r^2 = 0.40–0.70$) was greater than those for stand averages.

DISCUSSION

To understand the behavior of salmonberry in forest stands and to interpret its role in secondary succession, it is important to study both individual clones and populations of clones. Clones in our study sites were

irregular in shape; as individuals they had a loose network of rhizomes and a sparse canopy of aerial stems. When they coalesce, however, the resulting assemblage of rhizomes and ramets apparently maintains a dense cover that can have a profound effect on forest succession.

Persistence of salmonberry and implications for forest succession

Vegetative growth and replacement enables salmonberry to maintain a dense canopy that substantially inhibits regeneration of trees and taller shrubs. Aerial stems are continually recruited from two sources: (1) sprouts from the base of established ramets, and (2) new ramets arising from annual rhizome extensions that "fill in" unoccupied parts of the stand, replacing dead or nonproducing ramets. In addition, there is a large rhizome bud bank capable of shoot production
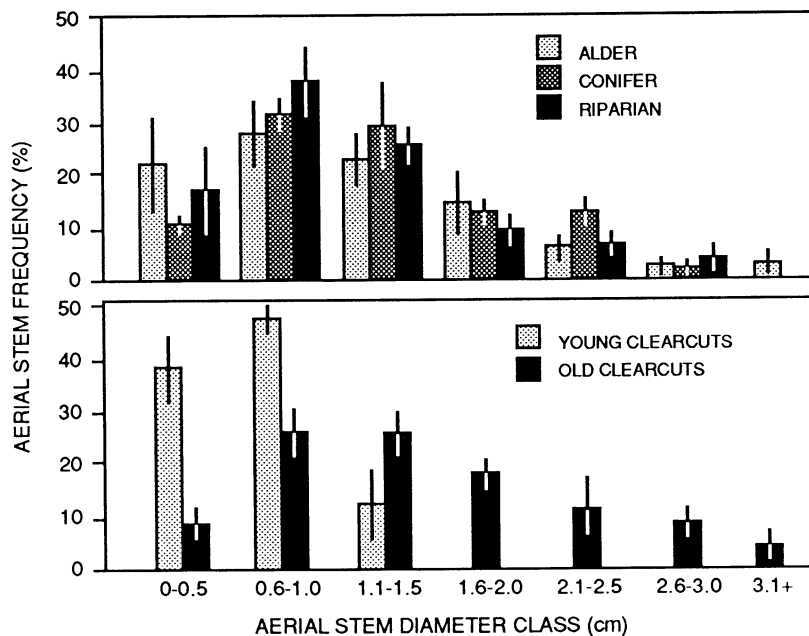
FIG. 4. Average salmonberry aerial stem population frequency, by stem diameter and class and stand type. Data are means ± 1 SE.

if aerial stems are killed. For example, in growth chamber experiments, estimates of preformed bud density were as high as 2 buds/cm of new rhizome; the production of adventitious buds may substantially increase bud density (J. Zasada, *personal observation*).

Even severe disturbance that kills all aerial stems and overstory trees does not necessarily affect salmonberry stability. Rather, aerial stem density increases from the bud bank in the rhizomes and at the base of aerial stems, from rhizome extension, and through production of new rhizomes (Fig. 3); within two growing seasons a new, denser cover >2-m tall results (Allen 1969). Thus, after disturbance, sprouting salmonberry can regrow rapidly and inhibit succession of other species rather than facilitating their establishment (Con-

nell and Slatyer 1977, West et al. 1981). Once a persistent salmonberry cover is established under alder or in the open, succession to other tree/shrub communities is unlikely without a severe disturbance and/or the presence of pathogens and insects that severely reduce the bud bank in the ramets and rhizomes (Franklin and Pechanec 1967, Carlton 1988).

The inverse relationship between overstory density and rhizome length (Fig. 5) and total biomass (Table 3) suggests that the population structure of salmonberry populations and clones is affected by the overstory. After disturbance, perhaps 15–25 yr are required for salmonberry to reach its peak biomass, provided there is no competition from overstory trees. The presence of upland and riparian conifers or alder decreases

TABLE 3. Regression equations relating salmonberry rhizome length and biomass and total biomass to overstory basal area and salmonberry basal area and stem density.

	r^2	$s_{y \cdot x}$ *	P
Rhizome length per unit ground area (m/m²)			
$\log y = 2.506 - 0.033 \text{OBA}$†	0.81	0.106	.001
$\log y = -0.209 + 0.670 \log \text{SBA}$‡ $+ 0.0234 \log \text{SSN}$§	0.73	0.395	.001
Rhizome biomass per unit ground area (kg/m²)			
$\log y = -3.426 + 1.159 \log \text{SBA}$	0.83	0.375	.001
Total biomass per unit ground area (kg/m²)			
$\log y = 2.00 + 0.490 \log \text{SBA} - 0.893 \log \text{OBA}$	0.78	0.270	.001
$y = 0.206 + 0.189 \text{SBA} - 0.047 \text{SSN}$	0.71	0.83	.01

* Standard error of estimate.
† OBA = Overstory basal area (m²/ha).
‡ SBA = Salmonberry basal area (cm²/m² at 15 cm above ground).
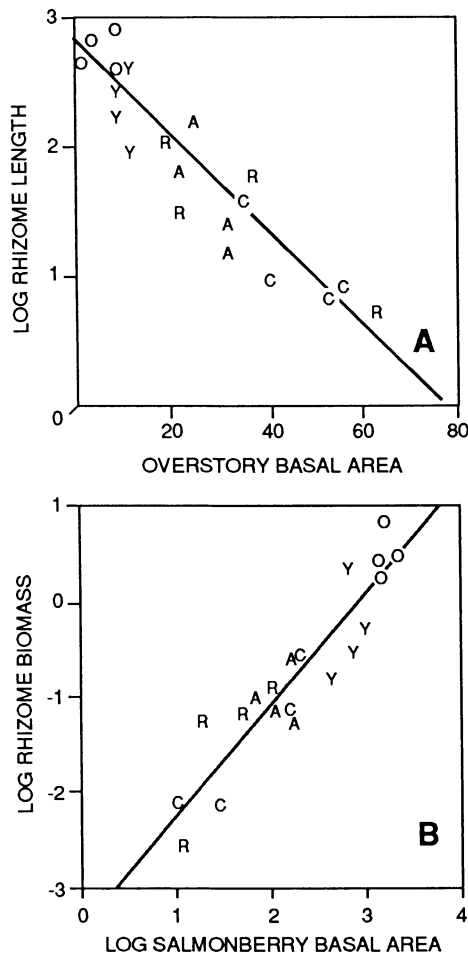§ SSN = Salmonberry stems (number/m²).

FIG. 5. The relationship of (A) rhizome length of salmonberry populations to overstory tree basal area, and (B) rhizome biomass of populations to salmonberry stem basal area at a height of 15 cm. Rhizome length was measured in metres per square metre of ground area, rhizome biomass in kilograms per square metre, and salmonberry basal area in square centimetres per square metre of ground area. See Table 3 for equations of the lines.

salmonberry biomass accumulation as the overstory canopies close. Under a high density of conifers, clones may die or may persist as small linear clones (Fig. 2, Table 2) in populations with low biomass (Fig. 3). Clonal expansion and development of cover probably occurs as conifers self-thin and conditions for understory development become more favorable.

Other woody rhizomatous shrub species have similar potential for establishing dense stable covers. For example, clones of beaked hazel (*Corylus cornuta* Marsh.), like salmonberry, support a range of aerial stem ages and sizes, and in undisturbed understories young stems are recruited by vegetative reproduction (Tappeiner 1971). Over a 19-yr period, Kurmis and Sucoff (1989) found that numbers of stems fluctuated, but the distribution of stems by size class was constant,

as was mean stem size. Thus, population structure of the hazel apparently stayed remarkably constant through recruitment of young stems and death of large old ones, resulting in a stable community. We think a similar process occurs in salmonberry stands. Size class distributions of hazel aerial stems were similar to an uneven-aged forest of trees (Smith 1986); they were nearly identical to those we found in salmonberry on old clearcuts, alder, conifer, and riparian stands (Fig. 4).

Clone size and structure

We observed a significant amount of variation in new rhizome extension occurring in salmonberry clones (Fig. 2). The greatest extension was measured in the youngest clearcuts; extension in the other stand types did not differ significantly among stands. Unlike clonal expansion in some species, new rhizome development in salmonberry is not limited to the periphery of the clone. Thus the bud bank increases at the interior of the clone and within stands of salmonberry as well as at the periphery. In addition, new aerial stems are initiated throughout salmonberry clones, as in clones of beaked hazel (Tappeiner 1971), rather than just at the advancing edge as in prickly ash (*Xanthoxylum americanum* Mill.) (Reinartz and Popp 1987). Thus clonal expansion, maintenance, and consolidation appear to be occurring simultaneously.

We generally support Bell and Tomlinson's (1980) conclusion that the immediate environment superimposes a regulatory response on the intrinsic pattern of the architecture of clonal plants. But our results strongly suggest that the belowground architecture of individual clones is affected more than aboveground architecture. Rhizome structure was related to overstory density; as overstory density decreased, structure ranged from nearly linear, with few ramets, to branched with many ramets (Table 2, Figs. 1 and 2). However, distribution of aerial stems by condition class did not vary among alder, conifer, or riparian stands. In recent clearcuts, of course, clonal structure both above and below ground was quite different from that in the other stand types because of the rapid and simultaneous initiation of new rhizomes, new ramets, and aerial stems on old ramets. The greatest variation in clonal architecture was found in clones in riparian zones where development was restricted by rocky substrate and water.

Most salmonberry clones excavated (84%) were intact; there was no evidence that rhizome death and the fragmentation of clones was a major process on our study sites. Rhizomes were living, and there was little evidence of decay. The largest rhizomes were 5–8 cm, a 10-fold or more increase in diameter over new rhizomes (0.5 cm). This increase suggests that continual activity of secondary meristems may promote rhizome health and longevity. Except in the clearcuts, there had been no apparent disturbance of these sites for over 45

yr; rhizomes seem able to remain intact for at least this long. Thus we conclude that salmonberry fits Reinartz and Popp's (1987) classification of woody clones that maintain viable connections, at least on open sites and under alder; in conifer stands, however, parts of clones (or entire clones) may decay as the canopy closes.

Individual salmonberry clones are fairly small compared with other reported shrub species; the maximum area for a single clone in our study was 50 m², and this area was occupied by other salmonberry clones as well. Maximum areas reported for other shrub species are 5 m² for beaked hazel (Tappeiner 1971), big huckleberry (*Vaccinium membranaceum* Dougl.) (Minore 1975), and Alaska blueberry (*V. alaskaense* Howell) (Tappeiner and Alaback 1989); 10–20 m² for prickly rose (*Rosa acicularis* Lindl.) (Calmes and Zasada 1982); 150 m² for prickly ash (Reinartz and Popp 1987); 250 m² for sandbar willow (*Salix interior* Rowles) (Krasney et al. 1988); and 800 m² for smooth sumac (*Rhus glabra* L.) (Gilbert 1966).

Salmonberry population structure

When studying clones, we were impressed with their differences, particularly differences in belowground structure among stand types. However, when we examined the populations formed by merged clones, we found them to be relatively similar. In alder, conifer, and riparian stands and in older clearcuts, size class distributions of aerial stems were nearly identical (Fig. 4), and in the three undisturbed stand types rhizome length, stem number, ramet density, and rhizome biomass were fairly similar (Fig. 3). In recent clearcuts, the structure of rhizomes and aerial stems in salmonberry populations, as in clones, differed substantially from that in undisturbed stands. Within 13 yr of disturbance, as stem density decreased (Fig. 3), new smaller aerial stems were produced, and the stem size/age distribution became similar to the distributions in the understories of alder, conifer, and riparian stands.

The greater light transmission through the open alder canopy probably explains the greater salmonberry biomass above ground in the understory of alder stands compared with that in conifer and riparian stands. In addition, salmonberry produces leaves earlier each spring than alder does, possibly allowing it to take advantage of the higher light availability before alder leaves have expanded (Barber 1976). We have no explanation for why salmonberry populations in alder stands had four times more biomass in aerial stems than in rhizomes, compared with a ratio of 2.5 for conifer, riparian, and older clearcuts. It is possible that reduced moisture stress, increased soil nitrogen on some sites, and sufficient light allow relatively greater aboveground production.

Distribution of biomass in salmonberry communities was similar to that of beaked hazel in the understory of northern conifer stands, where 30–40% of the total biomass was below ground (Tappeiner and John

1973). On unburned stands, prickly rose, which has small stems and rhizomes and generally lower stand densities than salmonberry, had ≈85% of its biomass in rhizomes; 75% on a 2-yr-old burn was in rhizomes (Calmes and Zasada 1982).

Modeling rhizome length would allow prediction of the magnitude of the budbank and help determine the response to various types of disturbance (Maxwell 1990). Our results suggest that it is realistic to model rhizome density. For example, the total length and/or biomass of rhizomes can be predicted from salmonberry aerial stem number or basal area and overstory basal area, which are easily measured aboveground parameters (Table 3, Fig. 5). Similarly, the rhizome biomass in beaked hazel populations can be predicted from aerial stem density (Tappeiner and John 1973).

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